

Extinction risk and structure of a food web model

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We investigate in detail the model of a trophic web proposed by Amaral and Meyer [Phys. Rev. Lett. **82**, 652 (1999)]. We focused on small-size systems that are relevant for real biological food webs and for which the fluctuations are playing an important role. We show, using Monte Carlo simulations, that such webs can be non-viable, leading to extinction of all species in small and/or weakly coupled systems. Estimations of the extinction times and survival chances are also given. We show that before the extinction the fraction of highly-connected species (“omnivores”) is increasing. Viable food webs exhibit a pyramidal structure, where the density of occupied niches is higher at lower trophic levels, and moreover the occupations of adjacent levels are closely correlated. We also demonstrate that the distribution of the lengths of food chains has an exponential character and changes weakly with the parameters of the model. On the contrary, the distribution of avalanche sizes of the extinct species depends strongly on the connectedness of the web. For rather loosely connected systems we recover the power-law type of behavior with the same exponent as found in earlier studies, while for densely-connected webs the distribution is not of a power-law type.

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I. INTRODUCTION

Food webs describe the resources and trophic relationships among species within an ecosystem. The first semi-quantitative descriptions of food webs were given by biologists at the end of the nineteen century [1, 2]. Later on prey-predator relationship between species were defined in terms of oriented graphs with hierarchical or layered structures [3]. The problem of describing such food webs was then taken over by mathematicians and physicists, and different modeling levels and types of models have been proposed.

A first group of models is constituted by the so-called *static models* in which the links between different species are assigned once and for all, according to different scenarios (random, scale-free or small-world graphs [4, 5], for example). Some properties of these food webs were analyzed and compared with available biological data, and the comparison usually turned out to be quite poor.

The second group of models contains the so-called *dynamic food web models*. The novelty consists in recognizing that the links between the species are generally not

arbitrary and quenched, but emerge as the result of some intrinsic biological dynamics. There are then many possibilities to model the evolutionary dynamics [6]. The simplest one concerns two-layered systems with prey-predator Lotka-Volterra type of dynamics (for a short review, see [7]). A very large body of work has been devoted to the study of population dynamics equations for more than two species [8, 9]. In such cases, the links among the species can be modified according to the evolutionary dynamics. One important issue is the control of the robustness of such models when the complexity of the system is increased. Moreover, at a more refined level of description, the Lotka-Volterra mean-field dynamics can be replaced by individual-based models [10, 11] taking into account the particularities of the interacting individuals and thus offering the possibility to include the stochastic fluctuations. These dynamic food webs models allow therefore to treat on an equal footing both the micro- and the macro-evolution of an ecosystem [12, 13].

The richness of the models mentioned above has its own drawbacks. Indeed, the number of control parameters defining the models is usually quite large; moreover the dynamics is nonlinear. Thus, it is often impossible to get a global picture of the properties of the system. Accordingly, it is desirable to study some models which are as simple as possible, in order to clarify the relative importance of the various ingredients, while being able to capture the generic properties expected for food

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webs. Several proposals have been made along this line in the past years, see e.g. [14, 15]. In particular, Amaral and Meyer [16] proposed such a “minimal” model whose numerical solution leads to a power-law distribution of extinction-avalanche sizes, in good agreement with available data from fossil record. It was shown later that this model is self-organized critical [17] and that the power law can be obtained analytically. Furthermore, taxonomic effects have been added to the model [18], but without significant effects.

In this work we are revisiting the Amaral – Meyer model (AM hereafter) with the aim of investigating several of its properties which are relevant for real food webs and which have not been addressed in the previous works. The paper is organized as follows. In Sec. II, the model is described and several technical details concerning the Monte-Carlo simulations, as well as the values of the control parameters, are given. Section III contains the main results. First, the dependence of the survival chance and of the average extinction time on the number of niches N and on the maximum number of feeding species k is studied. The problem of extinction due to stochastic effects is also discussed. Then the question of the pyramidal structure of the food web is approached. Time correlations between the occupied niches at different levels are investigated. The time evolution of the ratio of omnivores is also computed, both for viable and non-viable food webs. The distribution of food-tree sizes as a function of the values of N and k is found to exhibit different regimes. Finally, the problem of avalanches of species extinctions is revisited. In contradiction with previous results, it is found that strong deviations from simple power laws for the size distribution of these avalanches can be observed for large values of k . Some of our predictions are compared with real biological data and are found to be in good agreement. Conclusions are relegated to Sec. IV.

II. MODEL

The AM food web model consists of L trophic levels, each of them containing the same number N of niches, which can be either empty or occupied by a single species. Each species from level $l = 2, 3, \dots, L$ feeds on at most k ($k \geq 1$) species that are randomly selected from the level below, $(l - 1)$ (see Fig. 1). Therefore a species from level l is a predator for some species at the level $(l - 1)$, and at the same time it may be a prey for species from the level $(l + 1)$ (except for the species on the top level L , that have no predators, and the species on the bottom level $l = 1$ that have no preys).

The dynamics of the web is driven by the extinction and creation of species, as well as by the dynamically-related evolution of the trophic links between the species. Namely, at each time step (Monte Carlo step, MCS), one starts by randomly removing species from the basal level 1, with a given “extinction probability” p . When

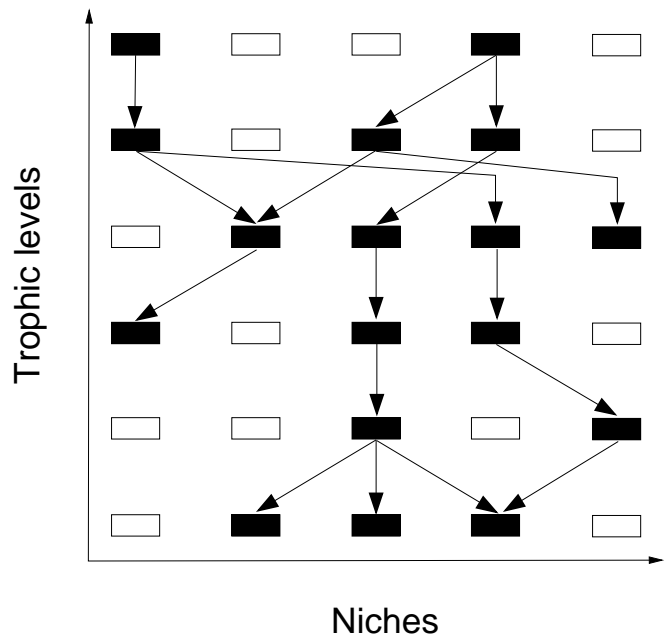


FIG. 1: Schematic representation of the AM food web model, for $L = 6$ and $N = 5$. The occupied niches are represented by the black rectangles and the interactions between species are depicted by the directed links.

a species gets extinct, all the links from it to species at the level 2 are removed. If as the result of these link removals a species at the level 2 loses all its preys from level 1, then it becomes extinct as well. This procedure of checking existing links and removal of species which lost all their food sources is then followed on each level till the top level L . Hence an avalanche of extinctions of species can be generated.

Apart from extinctions, the AM model considers also the creation of species in the free niches. Each species (that remains after the decimation procedure described above) at level l can repopulate, with a probability μ , an empty niche either at the level l , $(l - 1)$, or $(l + 1)$. New-created species receive at most k links, at random, to species from the adjacent lower level.

Extinction and creation of species are thus stochastic processes that differ from one realization of the food web to another, and one can address the question of the statistical properties of various characteristics of the system, like, for example, the size of the extinction avalanches, the extinction time (or, equivalently, the survival chance), the populations at all levels, the correlations between the different trophic levels, the density of the trophic links, etc. The dependence of these elements on the parameters of the model L , N , k , p , and μ is also an important aspect to be considered.

In this respect, the main result of the original paper [16] addressing the AM model was that the distribution of the sizes of the extinction avalanches can be fitted over about three decades by a power law with

an exponent $a \approx -1.98$; this exponent was corrected to the value $a = -2$ in later works [17, 18], which is supported by mean-field theoretical arguments. Moreover, it was argued that this power-law behavior is in agreement with available fossil data records. In Ref. [18] it has also been shown that the avalanche-size distribution exhibits a maximum for small-size events, before developing the power-law behavior. However, most of the characteristics of the food web that were enumerated above were not addressed in the previous papers on the AM model and our work is therefore intended to fill this gap.

We shall therefore investigate the AM model in more detail, by considering the canonical set of parameters used in [16], namely $L = 7$ trophic layers, the extinction probability $p = 0.01$ and the probability of creation $\mu = 0.02$. We shall moreover investigate how the system characteristics depend on the number of niches N and on the highest possible number of links k that a predator may have. The obtained results will be compared to experimental data coming from investigations of some contemporary food webs [19, 20, 21]. Since the total size – i.e., the product of the number of layers and the mean number of occupied niches – of the experimentally-observed food webs does not exceed 1000, we have decided to focus on N values that are smaller than the value of 1000 that was used in Refs. [16, 18], and to work with $N \leq 100$, exceptionally 200 and 500. As a consequence, the *role of fluctuations* in our systems becomes more important and many of the reported effects are clearly noise-induced and/or noise-affected, which actually makes them more relevant for real biological food webs. This choice of small N also allowed us to run the simulations for longer times than those considered in [16, 18], which unveiled new aspects of the food web viability. In general, we performed simulations over $\sim 10^6$ MCS and the averaging was done over 100 runs (i.e., random realizations of the food-web stochastic dynamics). In some cases, in order to check the viability of the system, we even went to $\sim 10^7$ MCS. Mean extinction times for the whole web were obtained by averaging over 500 runs.

III. MAIN RESULTS

A first result refers to the *viability* of the food web, i.e., to its capacity to survive in the long time limit. Performing much longer simulations than in [16, 18] we have found that small-size (e.g., $N = 50$ or $N = 70$) and weakly-coupled ($k = 3 - 6$) systems are not viable and disappear in the long time limit $t \approx 10^6$ MCS. Figure 2 illustrates how the chance that a web will survive till a given time t is depending on N and k . Survival chance at time t is defined here as the ratio of the number of realizations (runs) for which the system was still existing at time t , to the total number of trials. The web of $N = 100$ and $k = 3$ turns out to be non-viable, too (out of 100 runs, none has survived till 10^7 MCS), however increasing k to 4 stabilizes the system. The dependence of the

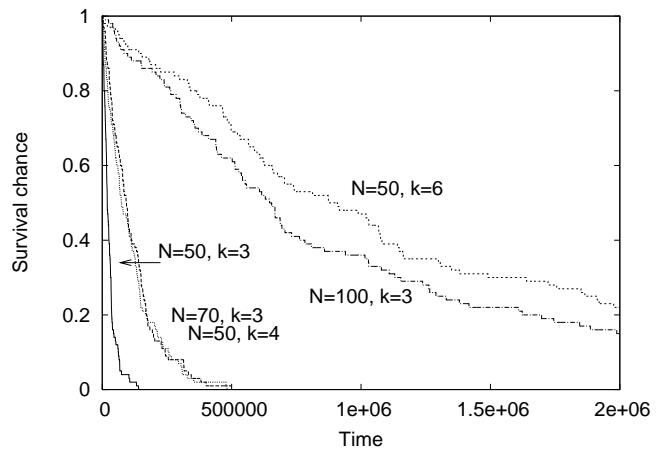


FIG. 2: Survival chance at time t for different values of N and k . Evaluated from 100 runs.

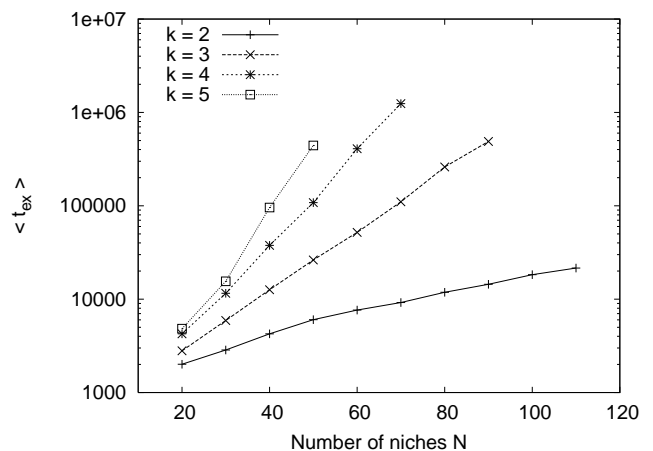


FIG. 3: Dependence of the average extinction time of the whole food web on N and k . The average was performed over 500 runs.

mean extinction time on the number of niches N , and on the maximum number of links k is illustrated in Fig. 3. It is obvious that increasing k , i.e., the connectedness, is stabilizing the web. Small, sparsely coupled webs cannot exist for a longer time.

The mechanisms leading to the collapse is connected with the stochastic nature of the extinction and proliferation events. Indeed, when the system is small, it may happen rather easily that at the lowest level, which is crucial for the survival of the web, only very few species survive. If, moreover, as is the case in the AM model, the values of the two creation and extinction probabilities, are very low, then two scenarios are almost equally probable, namely: (i) either some empty niches at the level 1 are repopulated and the web is, at least temporarily, safe, or (ii) existing species are all removed from this level, as illustrated in Fig. 4. This is the end of the food web,

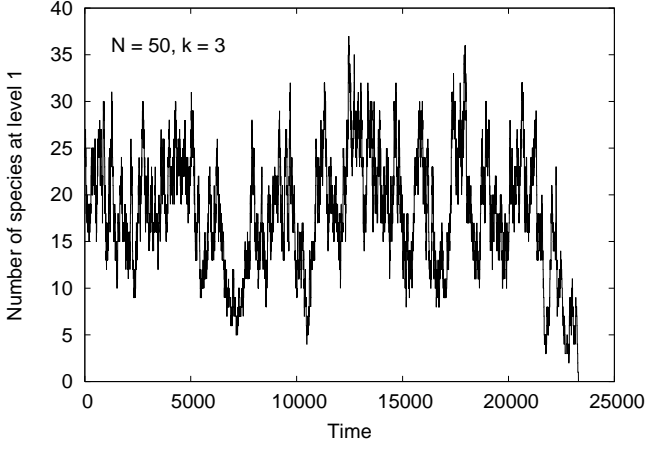


FIG. 4: Temporal evolution of the number of species on the basal level for $N = 50$, $k = 3$. Single run, exhibiting the complete extinction of the species on this level.

since without species at the basal level an avalanche containing all species is created and the web collapses. This *stochastic extinction* in small populations is a well known effect in ecology [22].

The next set of figures, see Figs. 5, illustrate the temporal evolution of the normalized populations at the different levels (i.e., the number of species at a given level divided by the total number of species in the web, at a given time). For the sake of clarity, only a part of the levels are shown. The AM model leads in a natural way to a *pyramidal form of the food web*, where the upper levels are less populated than the lower ones, see the upper panel. This effect is less pronounced when the system is close to its collapse, as shown by the lower panel of Fig. 5. Comparison with Fig. 6 indicates that the pyramid-effect is practically disappearing for systems with many niches (high N), and this is the reason for which it had not been observed neither in [16], nor in [18] for which $N = 1000$. Note also that the pyramidal structure has been best observed by biologists in rather small food webs [19].

As seen from both Figs. 5 and 6, the numbers of occupied niches at different levels are randomly oscillating in time. In order to check the *degree of correlation* of these oscillations, and whether there is some systematic time lag between them, we have calculated the correlation functions from the corresponding discrete-time series of the populations on the different levels, using the formula [23]:

$$C_{ij}(m) = C_i \begin{cases} \sum_{n=0}^{T-m} \delta N_i(n+m) \delta N_j(n), & \text{for } m \geq 0, \\ \sum_{n=0}^{T-|m|} \delta N_i(n) \delta N_j(n+|m|), & \text{for } m \leq 0 \end{cases}$$

Here $N_i(t)$ is the population of level $l = i$ at time t (which

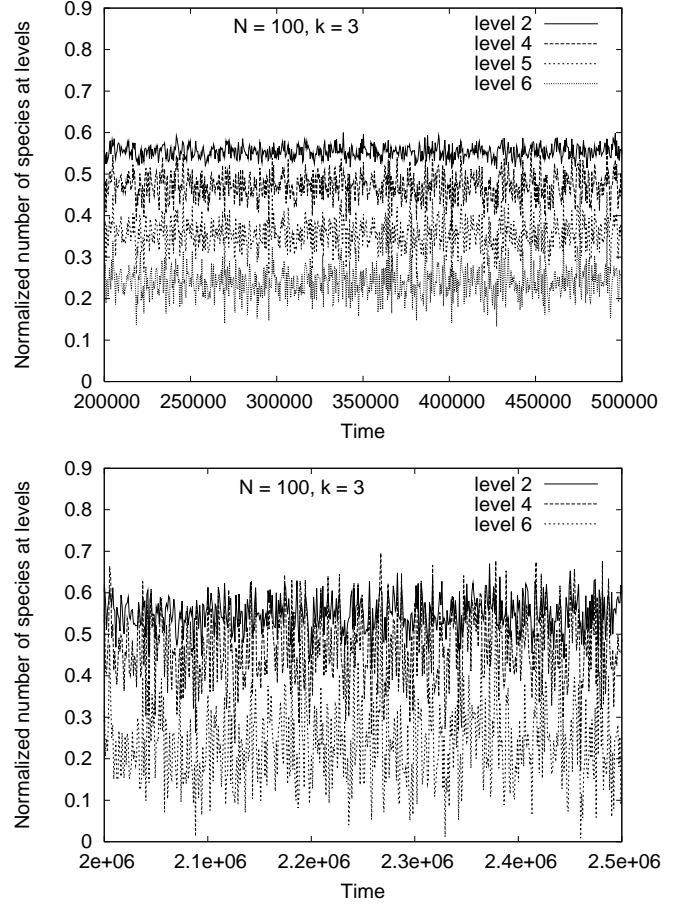


FIG. 5: Time dependence of the normalized populations of different levels for $N = 100$, $k = 3$. Upper panel: initial and mean time stage. Lower panel: long-time stage, just before the web collapse. Single runs.

is, of course, an integer number of MCS) and $\delta N_i(t)$ is its fluctuation around the mean value,

$$\delta N_i(t) = N_i(t) - T^{-1} \sum_{n=0}^T \delta N_i(n);$$

m is the time lag (that can be positive or negative), and T is the total simulation time. The coefficient C_i was chosen such that the autocorrelation functions at zero lag are equal to 1,

$$C_i = \left[\sum_{n=0}^T (\delta N_i(n))^2 \right]^{-1}.$$

The results for $N = 100$ and $N = 200$ are illustrated in Figs. 7 and 8, respectively. From these figures it follows that the time series at neighboring levels are highly correlated with each other at zero time lag. In other words, species at a given level adjust immediately to the changes at the level below, which is a feature that could

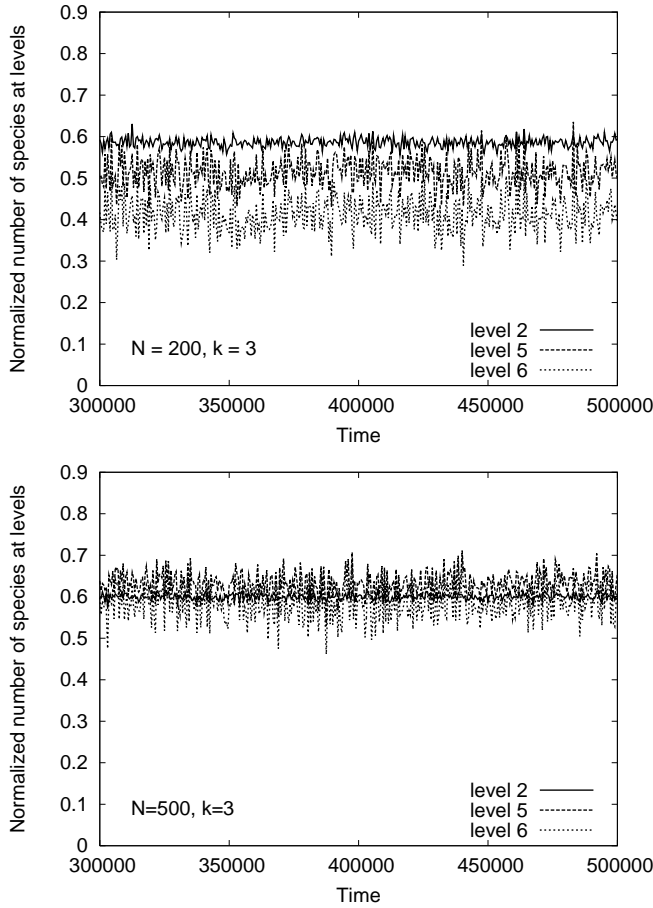


FIG. 6: Time dependence of the normalized populations of different levels for $k = 3$. Upper panel: $N = 200$. Lower panel: $N = 500$, single runs.

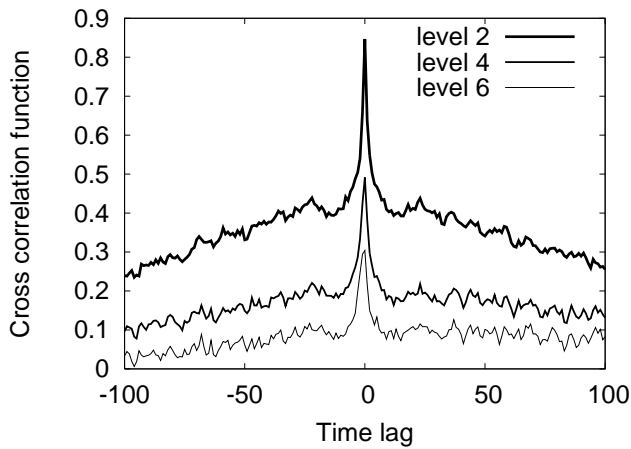


FIG. 7: Cross-correlations between the occupation numbers at levels $i = 1$ and $j = 2, 4, 6$. Here $N = 100$ and $k = 3$, and the evaluations are done on a single time-series.

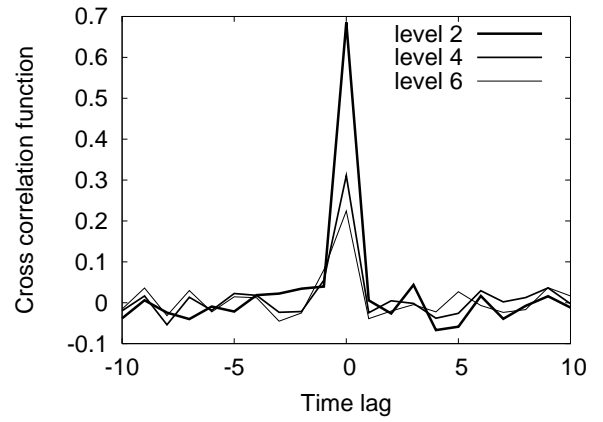


FIG. 8: Cross-correlations between the occupation numbers at levels $i = 1$ and $j = 2, 4, 6$. $N = 200$, $k = 3$, evaluations from single runs.

be expected in view of the constitutive dynamics of the model. The correlation is of course decreasing with the distance between the levels, but the peak at zero time lag remains. It should be noted that in the $N = 100$ case, Fig. 7, apart from the very narrow zero-lag correlation peak there is also a rather broad structure centered around it. This structure is practically absent in the case of the larger system with $N = 200$, see Fig. 8 and is to be related to the long-time instability of the system with $N = 100$ and $k = 3$, and to the strong fluctuations that are accompanying its collapse.

Another biologically interesting feature is the *fraction of omnivores*, that are predators feeding on more than one prey [24]. Figures 9 shows the distribution of the number of links per predator for a non-viable (upper panel), and a viable (lower panel) system, at several times. The distribution remains virtually the same throughout the simulation time for a viable web. However, for a non-viable one approaching extinction, the fraction of highly-connected predators grows. In other words, close to the collapse, only predators feeding on many preys will survive. In this sense, the presence of omnivores stabilizes the web, as documented experimentally in [24].

The average fraction of omnivores in a stationary state of the food web depends on the maximum value of links k , but it is rather insensitive to the number of niches N , as illustrated by the data in Table I. This feature also agrees with experimental results reported in [21].

In a stationary state of the web, the average number of links corresponding to different levels l has the same type of profile whatever the value of k , namely a more or less pronounced maximum for the intermediary levels and a drop for the low and top levels, as illustrated in Fig. 10.

Food webs are also often characterized by the *length of the food chains* (or “trees”) that are forming the web [19, 21]. We define them in the following way: each species

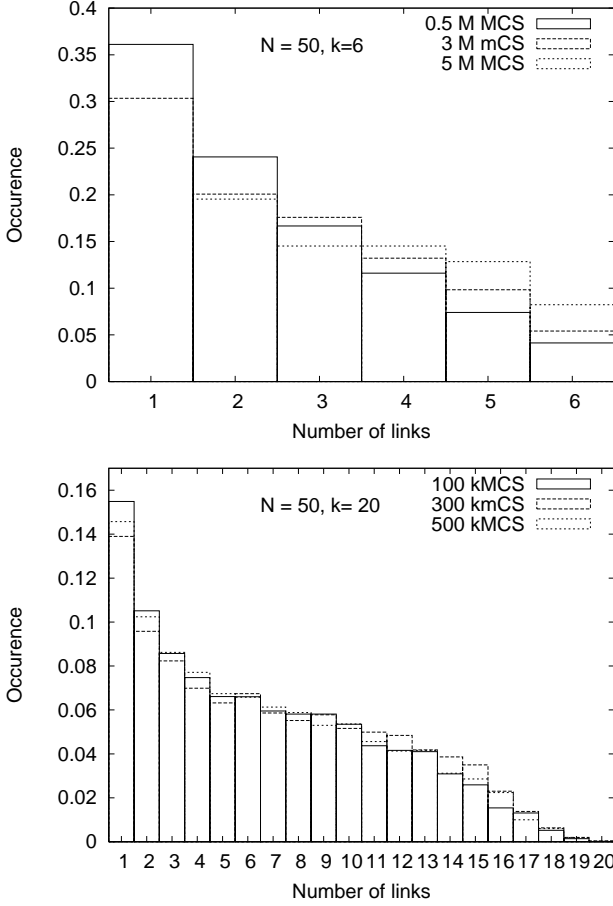


FIG. 9: Distribution of the number of links per predator for non-viable $k = 6$ (upper plot), and viable $k = 20$ (lower plot) systems, at different times. $N = 50$ in both plots, evaluations from single runs.

$N \backslash k$	3	4	6	20
50	0.312	0.4185	0.6966	0.8543
100	0.2936	0.4944	0.6567	0.8648

TABLE I: Average fraction of omnivores in a stationary state of the web, for various k and N . The average was taken over 100 runs.

with no predators is the root of a new tree. Starting from the root we go along its links to the lower level and mark all species the root is predating on. Then we check their links to find their prey species and so on. Since different predators do not really compete for food in the model (i.e., if they are linked to the same prey, they all get enough food), we can treat the partially overlapping trees as independent ones. The size of a tree is then simply the total number of species that belong to that tree.

As can be seen from Fig. 11, food tree size distribution

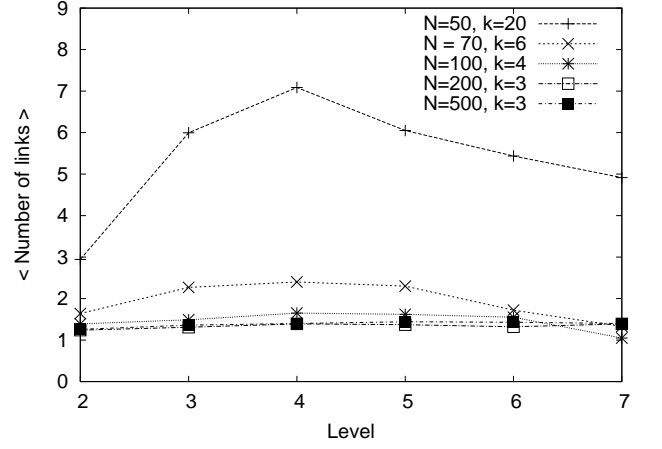


FIG. 10: Number of links for different levels in a stationary state of the web, averaged over 100 runs.

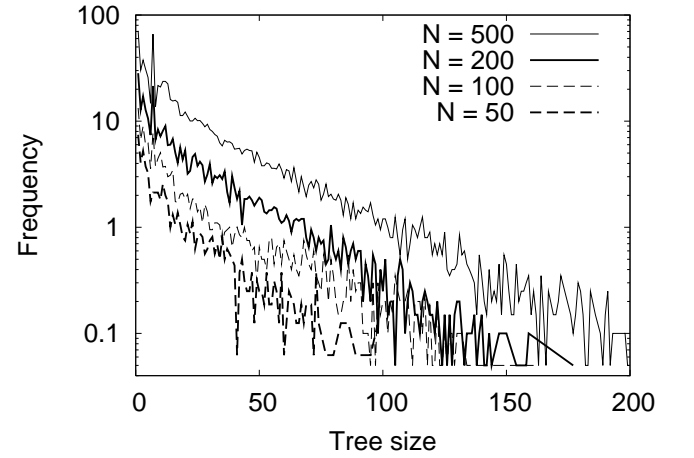


FIG. 11: Food tree size distribution at time $T = 3 \cdot 10^5$ MCS as a function of the number of niches N . $k = 6$, semi-logarithmic scale, evaluation from 100 runs.

depends on the number of niches N in the system. The maximal tree size increases with N , as could be expected. Moreover, in a bigger system there is more space for trees of similar sizes and that is why the curves in Fig. 11 shift upwards with increasing N . Linear dependence of the distribution of chain lengths on the semi-logarithmic plot in Fig. 11 indicates an exponential decrease with the tree size.

The maximum number of links k between species is also playing an important role on the food tree size distribution. The results for $N = 100$ niches at two different time steps are displayed in Fig. 12. When k increases, small trees become less likely and bigger structures in the system are preferred instead. We can thus distinguish two regimes with different k -dependence, namely the regime of “small trees” (of size ≤ 10), whose num-

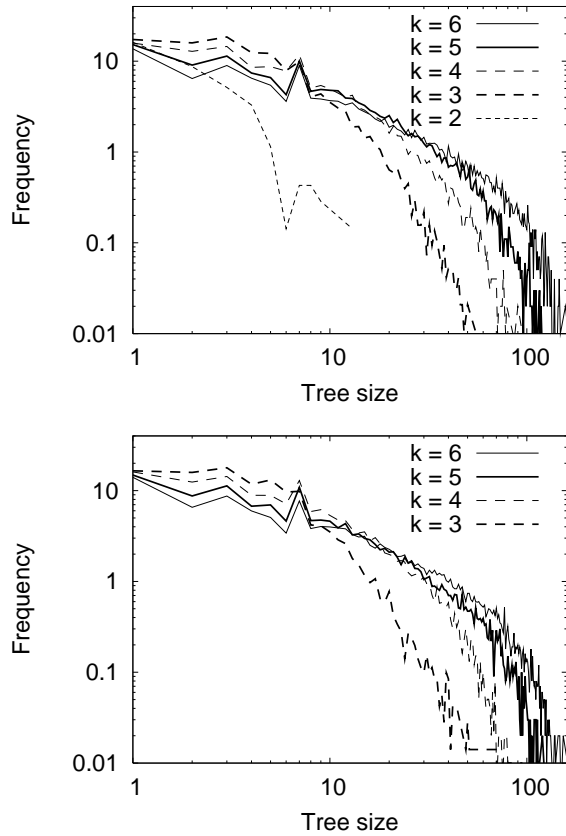


FIG. 12: Food tree size distribution at time $T = 5 \cdot 10^4$ MCS (upper plot) and $T = 3 \cdot 10^5$ MCS (lower plot) as a function of the maximal number of links between species k . $N = 100$, log-log scale, evaluation from 100 runs.

N	basal	interm.	top
100	0.16	0.79	0.05
200	0.10	0.80	0.10
500	0.12	0.79	0.09

TABLE II: Fraction of species at basal, intermediary and top levels. $k = 6$, average over 100 runs.

ber decreases with k , while the number of “big trees” is an increasing function of k . Moreover, the maximal size of a food tree varies strongly with k . It is also interesting to note that for sufficiently large N there is a well-pronounced peak in the distribution of tree sizes at a size of 7, which is simply the number of trophic levels in the system.

Biologists [1, 21] often describe food webs in terms of fractions of *basal*, *intermediate* and *top* species. In this model these ones correspond to occupied niches at levels 1, 2–6, and 7, respectively. For viable systems the values we obtain for these fractions are not too sensitive to the values of N and are presented in Table II. These results

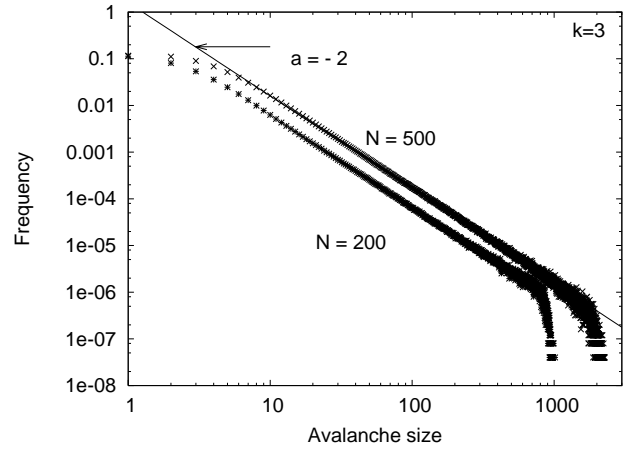


FIG. 13: Distribution of avalanche sizes for $N = 200$ and $N = 500$, for food webs with $k = 3$. Estimated from 500 runs.

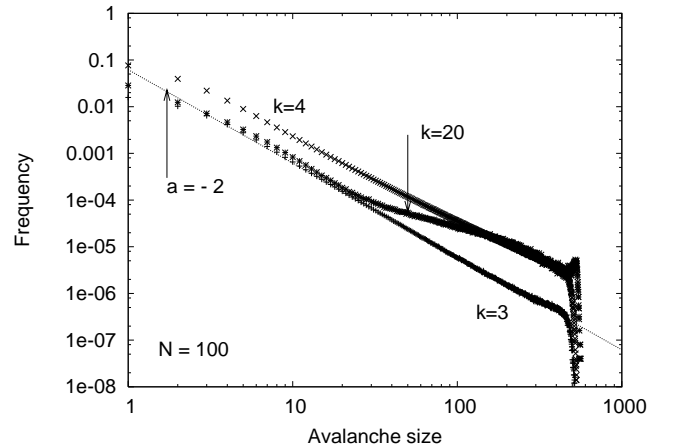


FIG. 14: Distribution of avalanches for $N = 100$ and different k . Estimated from 500 runs.

agree very well with biological data for a food web from Little Rock, U.S.A., see [21] for further details.

Finally, we have analyzed the distribution of *avalanche sizes of species extinctions*. We have observed the maximum in the distribution that was mentioned in [18], which becomes more pronounced with increasing the number N of niches. For $k = 3$, which was the value considered in [16, 18], we recovered the known power-law behavior, extending over nearly three decades, with an exponent equal to $a = -2$, as calculated in [17, 18]. This value does not seem to depend on N , and even for non-viable systems we got the same good fit to a power-law type of behavior, with the same exponent, see Figs. 13, 14.

However, when the food web becomes highly connected (i.e., $k = 6$ or larger) the deviations from the power-law behavior are very large, as illustrated in Figs. 14, 15 for $k = 20$. One may notice that for highly-connected webs

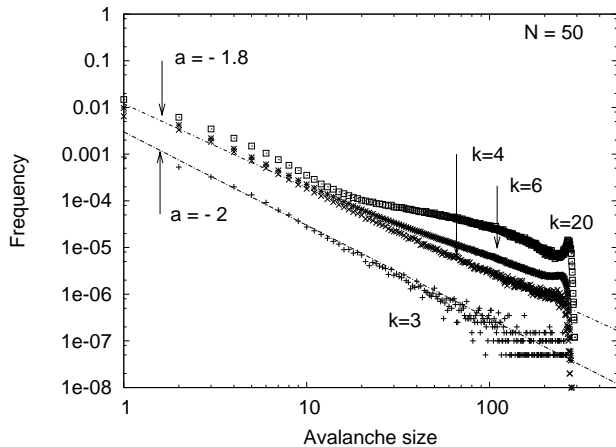


FIG. 15: Distribution of avalanches for $N = 50$ and different k . Estimated from 500 runs.

the fraction of larger avalanches increases, simply because the removal of a prey on which many predators feed is affecting more species.

As such, the power-law behavior, although largely present in the large- N webs, is *not universal*, but it is rather the result of a particular choice of the parameter values of the food web.

IV. CONCLUSIONS

We have presented a detailed discussion of several aspects of the AM model [16] of a food web that were neglected in the previous studies. In particular, we concentrated on relatively small-size systems and on the role the fluctuations can play in such systems, since this is the frame that is important in most of the real biological food webs. Several comparisons of the theoretical predictions with experimental data were also discussed.

Our simulations confirmed the observations of [18] concerning the distribution of avalanche sizes of species extinctions, the value of the power-law exponent $a = -2$, and the existence of a maximum depending on N . It is worth noting here that the same value $a = -2$ of the exponent of the distribution of extinction avalanches has also been found in two other different food web models,

Refs. [25] and [26]. The last paper is a generalization of the Bak and Sneppen model [27], in which two factors determine the fate of a species – biotic (“bad genes”) and abiotic (“bad luck”).

For reference, we have kept the values of some of the model parameters (number of layers L , probability of creation μ and of extinction p) the same as in the original AM model [16, 18]. However the dependence of the system behavior on the number of niches, N and on the maximum number of links per predator k , turned out to be quite interesting. We have thus unveiled new features of the model, not found in the earlier papers. A food web may collapse if it is too small and/or has not enough links between species. Systems smaller than $N \approx 200$ show a pyramid-like structure, where top levels are less populated than the bottom ones. The occupations of the levels are strongly correlated at zero time lag. When the web is close to a collapse, the fraction of highly connected predators (omnivores) significantly increases, which may lead sometimes to a (temporary) rescue of the web. The distribution of the length of food trees has an exponential character and its type depends rather weakly on both N and k . Finally, the distribution of species extinctions shows an unexpected feature, contrary to the previously-claimed universality of the power-law behavior; namely that for large k -values (i.e., highly-connected webs) the distribution cannot be described anymore as a power law.

Although several criticisms concerning the applicability of the AM model to biology have been raised [18, 28], we have found that some theoretical results, like the ratio of omnivores, the fraction of different-type (basal, middle, top) species, the food chain length etc., are in very good agreement with experimental data [19, 20, 21] on food webs. The significance of this fact is a subject of further analysis.

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